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## Progress Report

June 15, 1990 to June 14, 1991

#### Summary

This report covers our activities since June 15, 1990. The main accomplishments have been: 1) Continued experiments on the variation of color discrimination over color space, 2) Experiments on the influence of color on the perception of coherent motion, 3) Experiments on the effects of chromatic adaptation on color appearance, 4) Electrophysiological experiments on the effects of chromatic stimuli on the responses of neurons in the LGN and the visual cortex of macaque, and 5) The development of a new system for making displays for visual experiments on TV monitors which allows at least 12 bits of accuracy in the specification of the intensity of each of the three primaries.

#### Goals

The overall purpose of this project is to understand the contributions of chromatic mechanisms at various levels of visual processing to color vision, with particular interest in higher level mechanisms, that is, those beyond the conventional "second stage" mechanisms. Physiological experiments seeking to find the substrate for the psychophysical phenomena studied remain an integral part of the project.

#### **Progress**

## Psychophysics of color vision

We have continued to study the effects of chromatic adaptation on color discrimination. We have found, contrary to the previously accepted view, that the variation over color space of color discrimination follows very simple rules when care is taken to keep adaptation constant at the point in color space at which the discriminations are made. That these simple relations were not previously found can be understood from our findings that transient changes in adaptation profoundly effect color discrimination (Krauskopf, Williams and Heeley, 1982).

An important problem upon which these experiments have cast new light is where in the visual pathway do the processes underlying adaptation occur. One commonly held view is that the sensitivity of each class of cone receptors is regulated by the level of excitation of that class alone. Our experiments (Krauskopf and Gegenfurtner, 1990; and Krauskopf, Würger and Gegenfurtner, 1991) have shown that this explanation is neither necessary nor sufficient. On the one hand, we found that thresholds for the detection of pulses of light changing the input of the S cones only were elevated by increasing only the L and M cone excitation of the background showing that a change in the excitation of the S cones was not necessary to elevate the thresholds. On the other hand we found that thresholds for detecting changes along the L-M axis are constant failing to confirm the theory that the cone signals are of the form  $\frac{\Delta M}{M}$  and  $\frac{\Delta L}{L}$  which predicts that they should decrease when the relative contribution L cone input increases.

We completed a series of experiments on the role that chromatic mechanisms play in the perception of motion (Krauskopf and Farell, 1990). Drifting gratings modulated along different

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cardinal directions appear to slip with respect to one another. In contrast, when the directions of the modulations are rotated by 45 degrees in color space, the gratings cohere. We conclude that information about movement is conveyed to a high level in the processing chain within mechanisms maximally responsive along the cardinal directions.

## Color appearance changes resulting from chromatic adaptation

Asymmetric color matches were obtained under conditions of steady-state chromatic adaptation to lights of equal luminance differing either in L-M (red and green) or in S cone excitation (yellowish and bluish) from the standard equal-energy achromatic adapting light. The changes in color appearance induced by the transition from a grey to a chromatic adapting light is a measure for the effect of chromatic adaptation on the color appearance of the briefly presented test lights.

We tested the following hypotheses. Our first and most general hypothesis is that the changes in color appearance induced by the transition from an achromatic standard adapting light to a chromatic adapting light can be described as a linear transformation in three-dimensional color space. Our second and more specific hypothesis is that the color appearance changes resulting from chromatic adaptation are predicted by a coefficient law in cone excitation space, i.e. the color appearance changes are predicted by scaling the cone signals of the test light. Our third hypothesis is that a strong coefficient law holds in the cardinal direction space (Krauskopf, Williams & Heeley, 1982), i.e. we asked whether adapting lights differing only in L-M cone excitation result in appearance changes which require adjustment along the L-M cone axis only. And conversely, we asked whether adapting lights differing in S cone excitation only induce color changes which require adjustment along the S cone axis only.

We obtained the following results. First, adapting lights differing in S cone excitation only from the standard adapting light produced nonlinearities. For adapting lights varying along the L-M axis from the standard adapting light we did not find any deviations from linearity. Second, adapting lights differing in S cone excitation only from the standard adapting light produce color appearance changes which are inconsistent with a coefficient law, i.e. the color appearance changes of the test flash induced by yellowish and bluish adapting lights could not be accounted for by scaling the cone signals of the test light. For adapting lights varying along the L-M axis from the standard adapting light the results are compatible with a coefficient law, i.e. the color appearance changes resulting from red and green adaptation are predicted by scaling the cone excitations of the test light. However, the fact that adapting lights differing only in L-M cone excitation yield color appearance changes such that adjustment along the S cone direction is required, implies that the coefficients for at least two cone classes depend on the adapting input to the other cone classes. Third, the color appearance changes are inconsistent with a strong coefficient law in cardinal direction space. The color changes caused by adapting lights differing along the S cone axis only are not confined to this axis; similarly, adapting lights differing in L-M cone excitations produce appearance changes which require adjustment not only along the L-M cone axis but also along the S cone axis.

Furthermore, we found evidence that the adaptational effects, i.e. the induced color appearance changes, are not additive. Color appearance changes due to transition from grey to an adapting light differing in L-M as well as in S cone excitation (orange adapting light) could not be predicted by adding the color changes induced by adapting lights differing either along the L-M (red adapting light) or along the S cone axis (yellowish adapting light).

#### Electrophysiology of color vision

Collaborative electrophysiological research on color vision in Macaques with Peter Lennie of the University of Rochester continues. Our work which began with experiments on the lateral geniculate nucleus (Derrington, et al., 1984) and was pursued further in the primary visual cortex (Lennie, et al., 1990). DePriest, Lennie and I (1991) have been studying the effects of chromatic adaptation on the resting discharge and on the responses to chromatic pulses. These experiments relate directly to our psychophysical studies of chromatic discrimination. We have found that both the variability of the resting discharge and the amplitude of the responses to standard test stimuli vary with the locus of the adaptation field in color space in such a way to yield a constant signal-to-noise ratio. This surprising result is in accord with our psychophysical results which show that thresholds for discrimination along the "red-green" cardinal axis are invariant.

Programs have been written and used in collaborative experiments with J. A. Movshon of N.Y.U. on the responses of neurons in macaque areas V1, V2 and MT to chromatic and achromatic moving stimuli. The patterns used include both simple and compound ("plaid") gratings. The experiments seek to identify the substrate for the results on the perception of such stimuli obtained by Krauskopf and Farell (1990) discussed above. These programs provide for the generation of stimuli on a color TV monitor using an Adage frame buffer controller. The 68000 processor, incorporated in the Adage, which runs the programs also is linked to the computer which runs the physiological aspects of the experiment (collecting spike counts and analyzing them). This computer is able efficiently to request the presentation of the stimuli required by passing parameters and a numerical code requesting the particular class of stimulus needed.

## **Technology**

We have used an NIH Small Instrumentation Program grant to build a new general purpose device for producing experimental stimuli on color TV monitors. The new system was designed and constructed by Walter Kropfl of our center who also has developed a new Postscript like interpreter for use in controlling experiments. The new system allows control of the intensity of each of the three primaries of the color TV monitor in theory to 16 bits of accuracy. We have written calibration and experimental programs for the new system. We have found that in fact the accuracy of control is at least to 12 bits, or four times better than the nominal accuracy of the best systems on the market.

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